

FOLIAR TRICHOME VARIATION IN *QUERCUS* SECTION *PROTOBALANUS* (FAGACEAE)

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ABSTRACT

Foliar trichomes of *Quercus* section *Protobalanus*, the smallest section of the oaks, were studied using scanning electron microscopy. Distinct complements of non-glandular trichome types were observed for each of the five recognized species (*Q. cedrosensis* C.H. Müll., *Q. chrysolepis* Liebm., *Q. palmeri* Engelm. [*Q. dunnii* Kell.], *Q. tomentella* Engelm., and *Q. vaccinifolia* Kell.). Trichome characters fully support the current taxonomy of the section and provide additional characters for species identification. Intraspecific trichome variation was used to address both geographic variation and hypotheses of hybridization between several species-pairs. Contrary to previous reports, the total complement of non-glandular trichomes documented in section *Protobalanus* is as diverse as that observed in both the larger red (black) and white oak groups.

RESUMEN

Se estudiaron, mediante el microscopio electrónico de barrido, los tricomas foliares de *Quercus* sección *Protobalanus*, que es la sección más pequeña de los robles. Se observaron distintas cantidades de tipos de tricomas no glandulares en cada una de las cinco especies (*Q. cedrosensis* C.H. Müll., *Q. chrysolepis* Liebm., *Q. palmeri* Engelm., [*Q. dunnii* Kell.], *Q. tomentella* Engelm., y *Q. vaccinifolia* Kell.). Los caracteres de los tricomas apoyan la taxonomía aceptada de la sección y ofrecen caracteres adicionales para la identificación de especies. La variación intraespecífica de los tricomas se usó tanto para explicar la variación geográfica como para hacer hipótesis de hibridación entre varios pares de especies. Contrariamente a lo que se había citado previamente, la cantidad total de tricomas no glandulares en la sección *Protobalanus* es tan diversa como la observada en los grandes grupos de robles blancos y rojos (negros).

INTRODUCTION

Foliar trichomes provide a valuable set of analytical characters for species delimitation in *Quercus*. The use of trichome characters in *Quercus* dates back to the taxonomic studies of Camus (1936–54) and Dyal (1936), and their widespread application to oak taxonomy has increased through the use of scanning electron microscopy (SEM; e.g. Hardin 1975, 1976, 1979a, 1979b; Nixon & Steele 1981; Thomson & Mohlenbrock 1979). Many of the trichome differences visible under the SEM also are discernible with standard light microscopy (LM) or even a hand lens, but certain cryptic morphological differences, such as attachment of trichome rays, are better observed with SEM.

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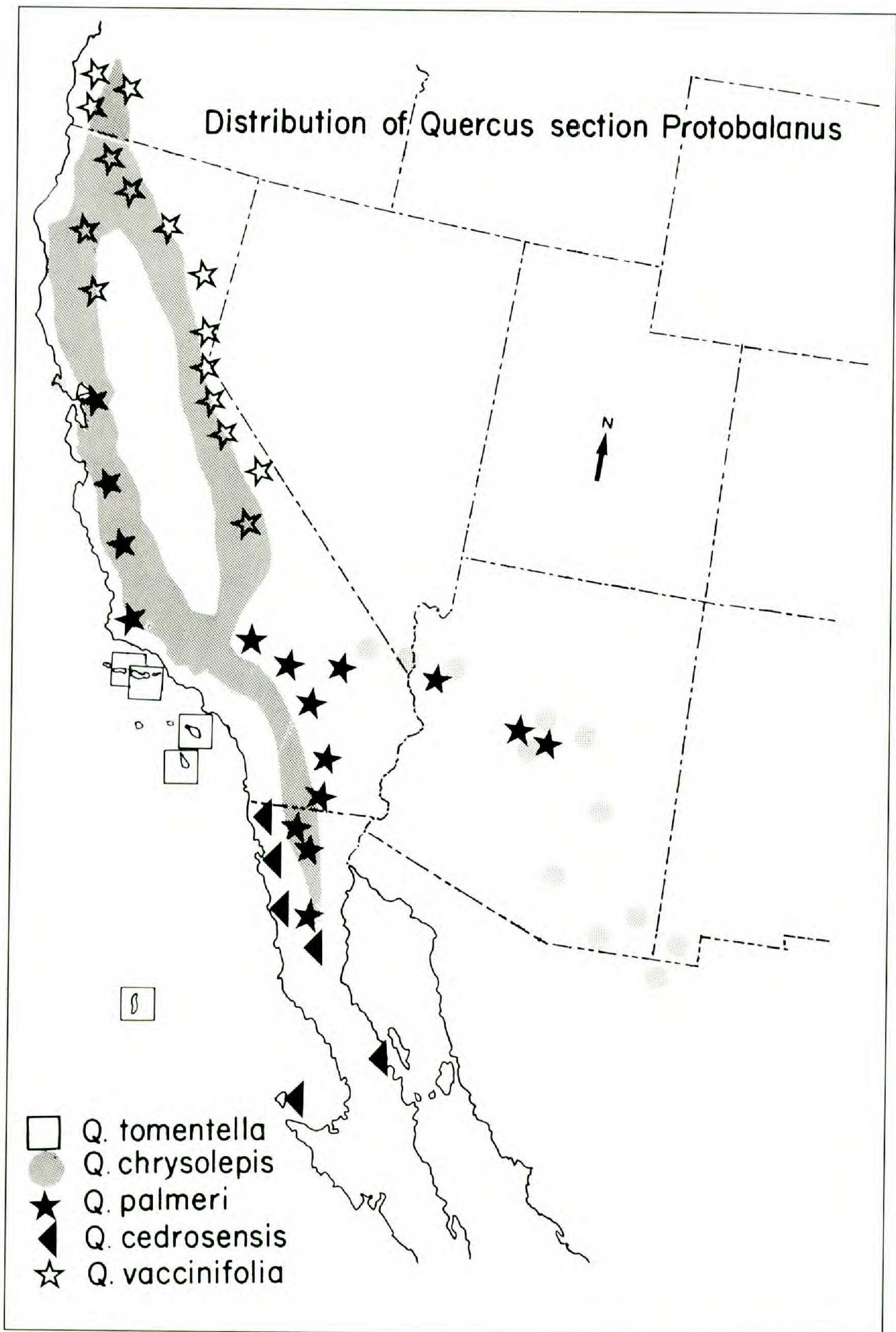


FIG. 1. Approximate distribution of *Quercus* section *Protobalanus*. The range of *Q. chrysolepis* is taken in part from Griffin and Critchfield (1972). The remaining species are mapped according to recent field and herbarium studies (Manos 1992).

The literature on the taxonomic use of trichome characters in *Quercus* ranges from the sectional and species-level to the identification of hybrids. Within certain sections of *Quercus*, trichomes may be of value in circumscribing at least some monophyletic groups. Other groups, however, such as the red oaks of eastern North America, show limited trichome diversity, and the delimitation of subgroups using trichomes alone is difficult (Hardin 1979a). Trichome type is a diagnostic character for a few putatively monophyletic species groups within the white oaks (section *Quercus*). The fused-stellate type found in all species of the “southern live oaks” (subsection *Virentes*) of the white oak group is one example.

Trichome characters have been used the most at the species level in the white oak group, and numerous examples of species-specific trichome complements have been documented in taxa considered to be closely related (e.g. Hardin 1979a, 1979b; Thomson & Mohlenbrock 1979; Nixon & Steele 1981). The identification of hybrids between white oak species has been addressed with patterns of trichome variation in many studies (e.g. Tucker & Müller 1958; Tucker 1963; Maze 1968; Cottam et al. 1982). These authors documented that hybridization between species can result in additive combinations of the trichomes of each species, in addition to modifications expected in other quantifiable characters.

Hardin (1976, 1979b) classified the trichomes of a fairly large sample of red and white oaks as 10 different types based primarily on glandularity, attachment, and ray morphology. Jones (1986), in his comprehensive treatment of foliar features of Fagaceae, discussed the distribution of trichome types found within the major groups of *Quercus* and recognized several more trichome types.

Quercus section *Protobalanus* (Trel.) A. Camus (golden-cup oaks or intermediate oaks), the smallest section of the three recognized within *Quercus* subgenus *Quercus* (Nixon in press), is restricted to western North America and consists of five species of shrubs and small to medium sized trees (Fig. 1). In previous descriptions of the morphology of the species of section *Protobalanus* (Engelmann 1876–1877, 1880; Trelease 1924; Müller 1962), trichomes were described superficially. These taxonomic treatments merely mention the relative density of leaf trichomes and no attempt was made to delimit species with trichomes. Jones (1986) recognized only three non-glandular types in section *Protobalanus*. According to his treatment, section *Protobalanus* has the least diverse complement of non-glandular trichome types of all sections of the genus.

My preliminary observations of herbarium, field collected, and greenhouse grown material of section *Protobalanus* have shown that LM is sufficient to discriminate the trichomes of the recognized species of section *Protobalanus*. Scanning electron microscopy, however, is very useful for illustrative purposes and to determine some fine detail not apparent with LM. These potential characters have not been quantified or described in any previous systematic studies of the group. The purpose of this study is to establish the extent of foliar

TABLE 1. Range and mean for quantitative features of trichomes types found in species of *Quercus* section

Protobalanus.

Species	Ray length (mm)		Number of Rays	
	Range	Mean	Range	Mean
<i>Q. cedrosensis</i> appressed-fasciculate	0.10–0.15	0.13	2–4	2.5
<i>Q. palmeri</i> fasciculate	0.18–0.25	0.20	5–12	8.3
<i>Q. tomentella</i> stellate	0.20–0.35	0.29	6–10	8.7
<i>Q. tomentella</i> multiradiate & fasciculate	0.37–0.60	0.52	3–10	7.2
<i>Q. chrysolepis</i> multiradiate	0.07–0.23	0.11	5–12	8.1
<i>Q. vaccinifolia</i> stellate & multiradiate	0.03–0.12	0.06	4–15	7.5

trichome diversity within section *Protobalanus* and to provide additional characters for species identification.

MATERIALS AND METHODS

The majority of specimens used in this study were obtained during several field trips to areas throughout the geographic range of section *Protobalanus* (Fig. 1). These collections represent population samples, most of which were used in other studies of morphological and molecular variation in section *Protobalanus* (Manos 1992). Additional herbarium material was examined at the following herbaria: ASC, DAV, SDM, UCSB, UCR, and SBBG. The Cornelius H. Müller Oak Herbarium (BH-CHM) was a rich source of material of section *Protobalanus*. The personal oak collection of Kevin C. Nixon, soon to be incorporated into BH, provided additional material for study.

Studies of trichome variation were conducted on individuals throughout the range of each species. A light microscope (40× and 200× magnifications) was used to determine trichome type and make observations for eventual calculations of range in ray length, mean ray length, range of ray number, and mean number of rays. These were calculated from 10 representative trichomes per individual examined (Table 1). Ray length was measured from the point of divergence of the ray and base of the trichome. Because samples were not random, standard deviations and confidence intervals were not calculated from these observations.

Following the initial survey of trichomes outlined above, specimens exhibiting typical species-specific trichomes were prepared for examination with SEM. This material was taken from herbarium specimens and dried, greenhouse-grown individuals and mounted onto aluminum stubs and sputter-coated with gold-

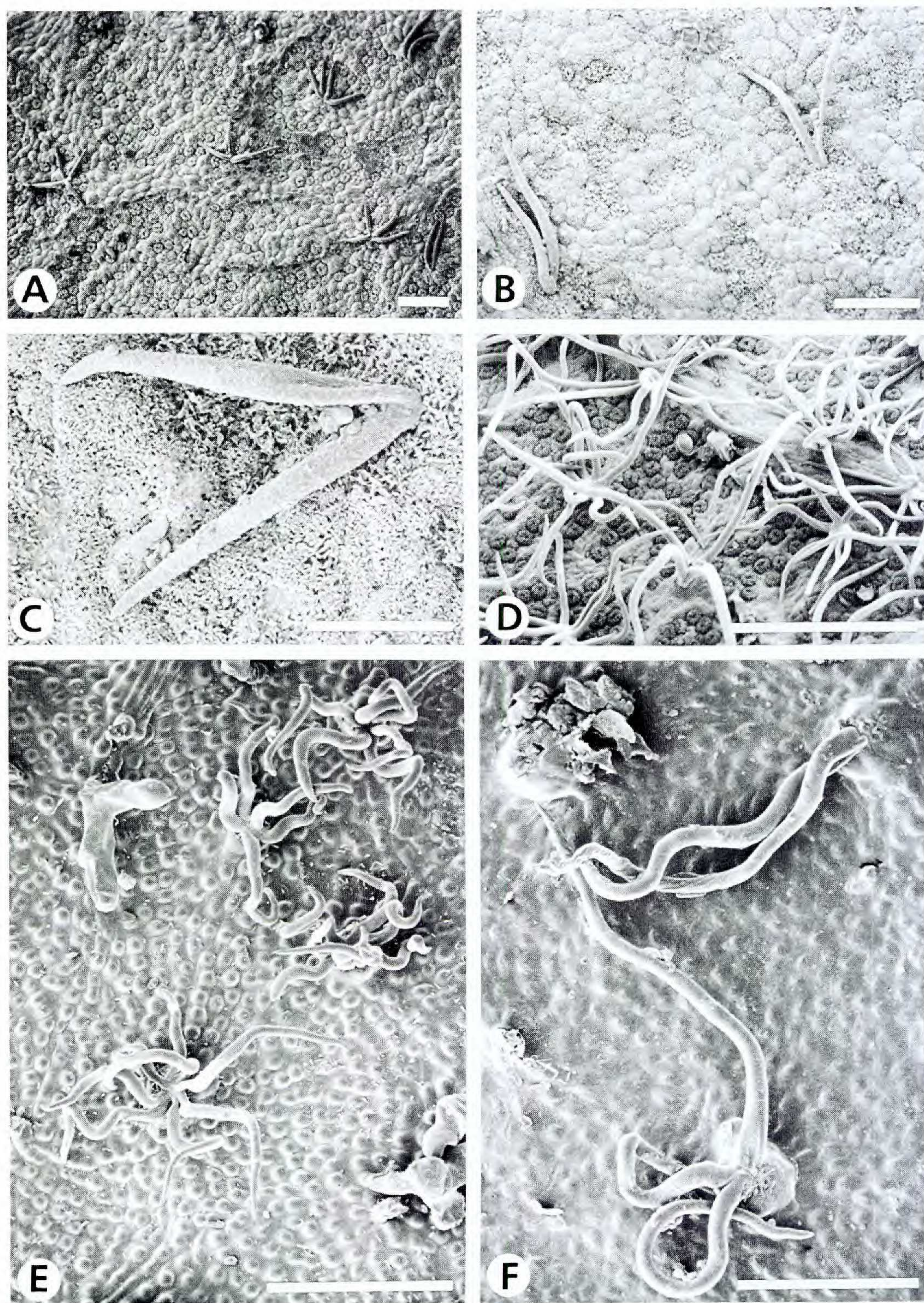


FIG. 2. SEM photographs. A) Appressed-fasciculate, *Q. cedrosensis*, scale bar = 100 μm ; B) appressed-fasciculate, *Q. cedrosensis*, scale bar = 100 μm ; C) appressed-fasciculate, *Q. cedrosensis*, scale bar = 50 μm ; D) fasciculate and stellate, *Q. tomentella*, scale bar = 300 μm ; E) fasciculate, *Q. palmeri*, scale bar = 200 μm ; F) fasciculate, *Q. palmeri*, scale bar = 100 μm .

palladium for 4 minutes in a Balzer's Union Sputtering Device. All leaf material was prepared without prior treatment or critical point drying. Trichomes pictured with SEM using the simple procedure outlined here do not deviate from typical trichome habit and morphology as observed with LM. An AMR 1000A SEM was used.

RESULTS

The descriptions which follow are representative of the mature condition of adaxial and abaxial leaf surfaces since mature leaves are most often collected for purposes of identification.

The currently recognized species within section *Protobalanus* (*Q. cedrosensis* C.H. Müll., *Q. chrysolepis* Liebm., *Q. palmeri* Engelm. [*Q. dunnii* Kell.], *Q. tomentella* Engelm., and *Q. vacciniifolia* Kell.) were distinguished by non-glandular, thick-walled trichome types. The distinction between *Q. chrysolepis* and *Q. vacciniifolia* was the weakest and based on observations that trichomes of *Q. vacciniifolia* predominantly are stellate, whereas trichomes of *Q. chrysolepis* exclusively are multiradiate. The trichome types found in both species were otherwise clearly differentiable from those seen in *Q. cedrosensis*, *Q. tomentella*, and *Q. palmeri* with both LM and SEM.

The non-glandular trichome complements on both adaxial and abaxial leaf surfaces within species of section *Protobalanus* were similar, and typically only differed in density. One exception is noteworthy. The trichomes of the abaxial surface (Fig. 2 H) of *Q. vacciniifolia* have fewer rays than those of the adaxial surface (Fig. 2 G). Table 1 lists, by species, the type(s) of trichome and includes descriptions of their respective morphology.

The golden glandular trichomes ("branched uniseriate" sensu Jones 1986; "simple branched" sensu Hardin 1976) commonly seen on the abaxial leaf surface, twigs and cupules of *Q. chrysolepis* and *Q. palmeri* are thin-walled and often collapse after drying (Fig. 2 F). Their absence in *Q. cedrosensis* and *Q. vacciniifolia*, combined with other characters, is taxonomically useful to discriminate each from *Q. chrysolepis*. The long solitary trichomes (Hardin 1976) also were observed on some specimens of all species; they are not taxonomically informative.

Descriptions of foliar trichomes of each species

Quercus cedrosensis C.H. Müll.

adaxial: leaf glabrous to puberulent; Types: appressed-fasciculate; no glandular trichomes.

abaxial (Figs. 2 A–C): leaf puberulent with epicuticular wax; Types: appressed-fasciculate and solitary; no glandular trichomes.

Appressed-fasciculate trichomes, persistent on the abaxial surface were diagnostic. This type clearly differs from the appressed-lateral type described by Hardin (1976). Appressed-fasciculate trichomes have not been reported in

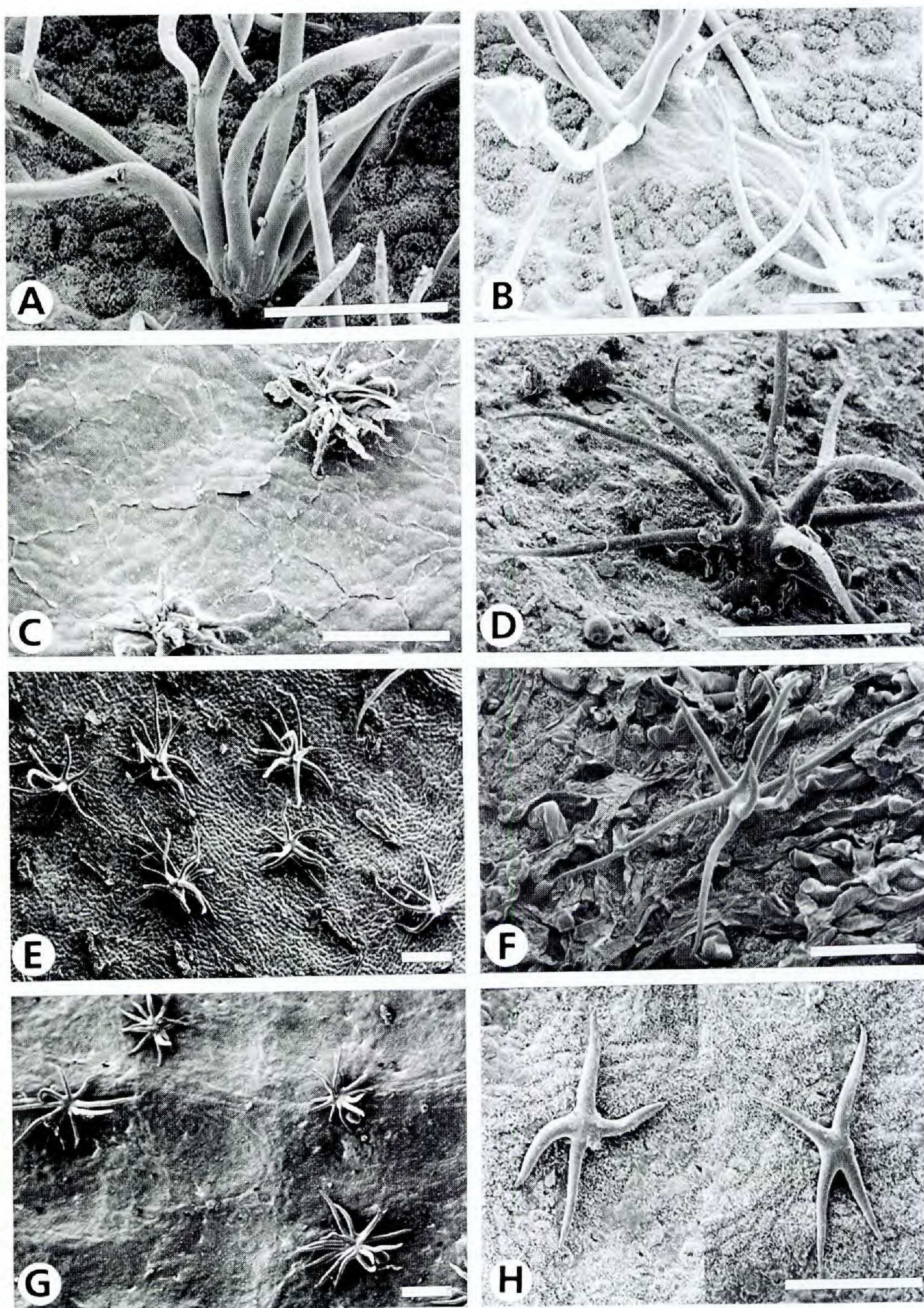


FIG. 3. SEM photographs, scale bars = 100 μ m. A) Fasciculate, *Q. tomentella*; B) fasciculate and stellate, *Q. tomentella*; C) rosulate, *Q. chrysolepis*; D) multiradiate, *Q. chrysolepis*; E) multiradiate and simple, *Q. chrysolepis*; F) multiradiate, simple-branched glandular, *Q. chrysolepis*; G) stellate and multiradiate, *Q. vaccinifolia*; H) stellate, *Q. vaccinifolia*.

Quercus. A cellular wall, only visible with LM, was observed between the rays of each 2-rayed unit. These paired trichomes might otherwise appear to represent a single-celled unit.

***Quercus palmeri* Engelm. [*Q. palmeri* Kell.]**

adaxial (Figs. 2 E, F): leaves puberulent; Types: fasciculate, solitary, and glandular.

abaxial: leaves puberulent to tomentose with epicuticular wax; Types: fasciculate and glandular.

Fasciculate trichomes, mostly persistent on the adaxial surface were diagnostic. The rays are erect, splay-out, twist near the apex, and insert on a distinct pedestal formed by the epidermis. Jones (1986) characterized this type as having rays that are joined only at the base.

***Quercus tomentella* Engelm.**

adaxial: leaf sparsely tomentose, mostly near the midrib; Types: fasciculate, multiradiate to stellate, solitary, and glandular.

abaxial (Figs. 2 D; 3 A, B): densely tomentose; Types: fasciculate, multiradiate to stellate, and solitary.

Fasciculate and multiradiate to stellate trichomes with long rays, persistent on the adaxial surface were diagnostic. A weak distinction between the types can be made by comparing the longer, erect fasciculate and multiradiate rays with the rays of the stellate type that are shorter and diverge laterally in one plane. The designation of the trichome complement in this species is somewhat arbitrary, because they appear to vary continuously, but this feature alone is diagnostic for *Q. tomentella*. The rays of these types are longer than those observed on the leaves of other species of section *Protobalanus*.

***Quercus chrysolepis* Liebm.**

adaxial (Fig 3 C–E): leaf puberulent; Types: multiradiate, rosulate, simple, and glandular.

abaxial (Fig. 3 F): leaf puberulent to lightly tomentose with epicuticular wax; Types: multiradiate, solitary, and glandular.

Multiradiate and rosulate trichomes, persistent mostly on the adaxial surface, were diagnostic. The multiradiate type was described by Hardin (1976) and Jones (1986) as being composed of approximately 8–12 rays that radiate in more than one plane from a typically rounded common base. The rosulate type also observed in this species seems to represent smaller and especially thin-walled multiradiate trichomes that collapse after drying (Fig. 3 C). They are most common on the adaxial surface of immature leaves that have been dried.

***Quercus vaccinifolia* Kell.**

adaxial (Fig 3 G): leaf glabrous to puberulent; Types: stellate to slightly multiradiate; no glandular trichomes.

abaxial (Fig. 3 H): leaf glabrous to puberulent with epicuticular wax; Types: stellate; no glandular trichomes.

Stellate trichomes were diagnostic, with an occasional upright ray, that approach the multiradiate type seen in *Q. chrysolepis*. The rays are shorter than those of *Q. chrysolepis* and parallel in attachment (Table 1). Stellate trichomes with fewer rays (ca. 4) observed on the abaxial surface also were diagnostic (Fig. 3 H). The ray length of these trichomes was within the range observed for the trichomes of the adaxial surface. The vestiture on the leaves and twigs of this species is often wanting or falls off soon after leaf expansion. On occasion, glandular trichomes were found on individuals collected from lower elevations. This feature is presumably the result of hybridization with *Q. chrysolepis* (Myatt 1975). The 4-rayed stellate trichomes of this species are easily distinguished from those of *Q. cedrosensis*, which often occur as two adjacent pairs of two-rayed trichomes. The rays in *Q. vaccinifolia* always diverged from a common point and are neither laterally-appressed nor composed of 1-rayed or 2-rayed units, as observed in *Q. cedrosensis*.

DISCUSSION

Species delimitation

The non-glandular trichomes of *Quercus* section *Protobalanus* are useful taxonomic characters that consistently delimit previously recognized taxonomic species. Qualitative variation in foliar trichomes provides, in most cases, unambiguous criteria for identifying the species of section *Protobalanus*. However, the distinction between *Q. chrysolepis* and *Q. vaccinifolia* is not based on a constant fixed difference, but rather on a strong trend toward stellate trichomes with shorter rays in *Q. vaccinifolia*. Trichome characters, in conjunction with fixed differences observed in other morphological characters (Manos 1992), can be used to diagnose distinct clusters of populations within section *Protobalanus* that correspond to taxonomic units as defined upon application of a phylogenetic species concept (sensu Nixon and Wheeler 1990).

Intraspecific variation

The majority of within-species trichome variation in *Quercus* is largely in the form of density or persistence (Hardin 1979a; Thomson and Mohlenbrock 1979). Many oak species possess a diagnostic trichome complement; therefore, deviations from a particular complement can be used as an indicator of either hybridization (e.g. Tucker 1963; Hardin 1975) or presence of a cryptic species (e.g. Nixon and Steele 1981).

The trichome complements observed for each species of section *Protobalanus* were relatively uniform in type, although variation in density and ray length, as

well as occasional intergradation between certain types was observed (see *Q. tomentella*). Hardin (1979a) discussed trichome variation in relation to habitat differences and suggested that the oaks of eastern North America showed greater pubescence in drier habitats. Among species of section *Protobalanus*, significant habitat diversity is observed within the ranges of *Q. cedrosensis* and *Q. chrysolepis*.

Multiradiate trichomes were found to be uniformly present throughout the range of *Q. chrysolepis*, with occasional variation in density. At the more mesic locality of Point Reyes, California, the trichomes were more dense than usual and had longer rays accounting for the higher values of ray length within the species, but were otherwise similar to the typical multiradiate type. The trichomes of individuals of *Q. cedrosensis* were identical from habitats on Cedros Island and inland Baja California (ca. 3000 ft) and from more mesic sites on the coast of Baja California (ca. 300 feet). In section *Protobalanus*, greater density of non-glandular trichomes apparently is not correlated with drier habitats. In the case of *Q. chrysolepis*, a few low elevation coastal populations appear to possess a greater density of non-glandular trichomes. The best example demonstrating the correlation of greater density of non-glandular trichomes and mesic habitats in section *Protobalanus* would be *Q. tomentella*, the island oak.

The taxonomic identities of populations from the extremes of the range of section *Protobalanus* are critical to establishing the limits of species boundaries, in addition to the discovery of where these boundaries may break down. One example that Müller (1962) alluded to is the putative *Q. chrysolepis* of the Sierra San Pedro Martir of Baja California, Mexico. These populations have small leaves reminiscent of *Q. cedrosensis*, and small, thin cupules resembling those of *Q. vaccinifolia*. All specimens available from this locality possessed only the typical multiradiate trichomes of *Q. chrysolepis*; therefore, this pattern of morphological variation is best considered intraspecific, and similar to other extreme forms observed in more northern high-elevation populations of *Q. chrysolepis*, rather than the result of past hybridization, as there is no evidence of either a combination of trichome complements or intermediate types.

Hybridization

It has been suggested that hybridization between *Q. chrysolepis* and *Q. palmeri* has occurred in populations of Arizona (Tucker & Haskell 1960; Myatt 1975). In this region, individuals have been variously assigned to *Q. chrysolepis*, *Q. palmeri*, or hybrids, but "pure" *Q. palmeri* is apparently absent based on morphological analysis of vegetative characters (Tucker & Haskell 1960; Manos 1992) and allozyme characters (Manos 1992). Examination of the trichomes present on numerous specimens collected throughout this region also supports the conclusion that "pure" *Q. palmeri* is absent, as only the multiradiate trichomes of *Q. chrysolepis* were observed. Based on other morphological characters (Tucker &

Haskell 1960), a hybrid origin for some of these individuals can not be ruled out; however, repeated backcrossing to *Q. chrysolepis* may have resulted in the loss of an intermediate trichome type or combined complement of types.

Hybridization between *Q. tomentella* and *Q. chrysolepis* has also been invoked to explain the intermediate vegetative features of many individuals on the Channel Islands of San Clemente, Santa Cruz (Manos 1992), and Santa Catalina (Thorne 1967). Examination of the trichomes present on this material supports other morphological evidence, as a novel combination of foliar vestiture was observed on several individuals that seemingly had an intermediate morphology. The following additive combination of trichome complements and densities was observed: 1) adaxial multiradiate trichomes with intermediate ray lengths, 2) abaxial fasciculate and stellate trichomes of *Q. tomentella*, but with shorter rays, 3) an appreciable adaxial cover of glandular trichomes, common in *Q. chrysolepis*, but usually absent on the mature leaves of *Q. tomentella*, 4) a pilose midrib consisting of solitary non-glandular trichomes, common in *Q. tomentella* and absent in *Q. chrysolepis*.

Limitations

An obvious drawback to the use of trichomes in the identification of species of section *Protobalanus* is their deciduous nature. Although many of the mature leaves of species of section *Protobalanus* appear to be devoid of non-glandular trichomes, I have found that a careful examination of first or second year leaves often results in the recovery of some trichomes. The trichomes of *Q. vaccinifolia* are sporadically present, because this species often produces either glabrous leaves or immature leaves that quickly lose their trichomes. This feature alone is often enough to recognize *Q. vaccinifolia*. The combination of stellate trichomes, if available, with other characters of the species is usually reliable evidence for identification of *Q. vaccinifolia*.

Affinities of section *Protobalanus* trichomes

In addition to the taxonomically uninformative solitary trichomes observed on most species of section *Protobalanus*, I have documented four taxonomically useful non-glandular trichome types. This is two more than reported by Jones (1986), who failed to recognize the presence of multiradiate and appressed-fasciculate types within the section, in his summary of the distribution of trichome types within *Quercus*.

Section *Protobalanus* possesses a similar diversity of trichome types when compared to larger groups of *Quercus*. This is somewhat surprising considering its small size and narrow distribution. Jones (1986) stated that trichome complements do not permit recognition of the sections within *Quercus*; however, his underestimate of the trichome types within *Protobalanus*, a small group, weakens my confidence in his appraisal of the other, more speciose sections and of the genus

as a whole. Because of the great importance of trichomes to oak taxonomy, a review of trichome diversity in *Quercus* and revised classification of trichome types is needed.

Hardin (1979) presented some generalizations concerning patterns of variation in trichomes between eastern North American red (black) and white oaks and their phylogenetic implications. Red oaks tend to have trichomes of the thick-walled multiradiate type and thin-walled rosulate type. The rosulate type appears to represent thin-walled multiradiate trichomes that collapsed upon drying. The predominant types within the white oaks are fasciculate and stellate. This assessment generally holds true for oak species from other regions (Nixon personal communication). While this pattern is relatively constant, certain exceptions are sure to be encountered. As observed here, multiradiate trichomes occur on *Q. chrysolepis*, while the other types observed in the section are commonly present in both red and white oaks. The trichome complement within section *Protobalanus* has a combination of types typically observed in other sections of *Quercus*. Other morphological characters of section *Protobalanus*, such as the frequent lateral position of abortive ovules in mature fruit, also appear intermediate relative to the condition observed in red (apical abortive ovules) and white (basal abortive ovules) oaks. Although a hybrid origin for the section remains a possibility, morphological and molecular investigations have not provided additional evidence in support of this hypothesis (Manos 1992). The apparent intermediate morphology of section *Protobalanus* led Trelease (1924; subg. *Protobalanus*) to hypothesize an ancestral relationship for the section with respect to both red and white oak groups. Recent cladistic analysis of *Quercus* (Nixon 1985, in press), however, supported a sister group relationship for section *Protobalanus* and the white oaks (section *Quercus*, E & W hemisphere), whereas the red oaks occupy a more basal position. According to that phylogenetic analysis, section *Protobalanus* shares ancestral character-states with the red oaks and derived character-states with the more closely related white oaks (section *Quercus*).

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REFERENCES

- CAMUS, A. 1936–1954. Les Chenes. Monographie du genre *Quercus*. Encyc. Econ. Sylvic., Vol. I, II, III. Lechevalier, Paris.
- COTTAM, W.P., J.M. TUCKER, and F.S. SANTAMOUR. 1982. Oak hybridization at the University of Utah. State Arbor. Utah Publ. No. 1.

- DYAL, S.C. 1936. A key to the species of oaks of eastern North America based on the foliage and twig characters. *Rhodora* 38:53–63.
- ENGELMANN, G. 1876–1877. About the oaks of the United States. *Trans. Acad. Sci. St. Louis* 3:372–400; 539–543.
- . 1880. Fagaceae. In: WATSON, S. *Botany of California*. Vol 2. John Wilson and Son, University Press, Cambridge.
- GRIFFIN, J.R. and W. CRITCHFIELD. 1972. The distribution of forest trees in California. U.S.D.A Forest Service Res. Paper PSW-82. 114 p.
- HARDIN, J.W. 1975. Hybridization and introgression in *Quercus alba*. *J. Arnold Arbor.* 56:336–363.
- . 1976. Terminology and classification of *Quercus* trichomes. *J. Elisha Mitchell Sci. Soc.* 92:151–161.
- . 1979a. Patterns of variation in foliar trichomes of Eastern North American *Quercus*. *Amer. J. Bot.* 66: 576–585.
- . 1979b. Atlas of foliar surface features in woody plants, I. Vestiture and trichome types of Eastern North American *Quercus*. *Bull. Torrey Bot. Club* 106: 313–325.
- JONES, J.H. 1986. Evolution of the Fagaceae: the implications of foliar features. *Ann. Missouri Bot. Gard.* 73: 228–275.
- MANOS, P.S. 1992. Cladistic analyses of “higher” Hamamelididae and Fagaceae, and systematics of *Quercus* section *Protobalanus*. Ph.D. dissertation. Cornell University, Ithaca, NY.
- MAZE, J. 1968. Past hybridization between *Quercus macrocarpa* and *Quercus gambellii*. *Brittonia* 20: 321–333.
- MÜLLER, C.H. 1962. A new species of *Quercus* from Baja, California, Mexico. *Madroño* 16: 186–192.
- MYATT, R.G. 1975. Geographical and ecological variation in *Quercus chrysolepis* Liebm. Ph.D. dissertation. University of California, Davis.
- NIXON, K.C. 1985. A biosystematic study of *Quercus* section *Virentes* (the live oaks) with phylogenetic analyses of Fagales, Fagaceae and *Quercus*. Ph.D. dissertation. University of Texas, Austin.
- . In press. Infrageneric classification of *Quercus* (Fagaceae) and typification of sectional names. *Ann. Sci. Forest.*
- and K.P. STEELE. 1981. A new species of *Quercus* from southern California. *Madroño* 28: 210–219.
- and Q.D. WHEELER. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6:211–223.
- THOMSON, P.M. and R.H. MOHLENBROCK. 1979. Foliar trichomes of *Quercus* subgenus *Quercus* in the Eastern United States. *J. Arnold Arbor.* 60:350–366.
- THORNE, R.F. 1967. A flora of Santa Catalina Island, California. *Aliso* 6:1–77.
- TRELEASE, W. 1924. The American oaks. *Mem. Natl. Acad. Sci.* 20:1–255.
- TUCKER, J.M. 1963. Studies in the *Quercus undulata* complex. III. The contribution of *Q. arizonica*. *Amer. J. Bot.* 50:699–708.
- and H.S. HASKELL. 1960. *Quercus dunnii* and *Q. chrysolepis* in Arizona. *Brittonia* 12:196–219.
- and C.H. MÜLLER. 1958. A reevaluation of the derivation of *Quercus margaretta* from *Quercus gambellii*. *Evolution* 12:1–17.